

FURTHER OBSERVATIONS ON THE MORPHOLOGY OF *WAKALEO VANDERLEUERI* (MARSUPIALIA:THYLACOLEONIDAE) FROM THE MID-MIOCENE CAMFIELD BEDS, NORTHERN TERRITORY

PETER MURRAY¹ AND DIRK MEGIRIAN²

¹*Northern Territory Museum of Arts and Sciences,
GPO Box 2109, Alice Springs NT 0871, Australia.*

²*Northern Territory Museum of Arts and Sciences,
GPO Box 4646, Darwin NT 0801, Australia.*

ABSTRACT

We describe new *Wakaleo vanderleurei* material from the Bullock Creek Local Fauna that gives an improved estimation of the range of variability of the species. The morphological bases for the discrimination of the species *W. vanderleurei* from *W. oldfieldi* are not as consistent as previously thought, but the distinction could continue to be retained as a chronospecies designation. The Late Miocene *Wakaleo alcootaensis* shows no tendency to overlap with *W. vanderleurei* at the large end of the morphocline. A distal radius fragment assigned to *Wakaleo* is described. The wrist joint of *Wakaleo* was less mobile than that of *Priscileo* Rauscher, 1987. A brief review of the phylogenetic relationships of the Thylacoleonidae and a consideration of the position of the wakaleonines based on the described material is given.

KEYWORDS: Thylacoleonidae, *Wakaleo* species, biochronology, systematics, morphology.

INTRODUCTION

The Thylacoleonid species *Wakaleo vanderleurei* (Clemens and Plane, 1974) was based on a dentary fragment containing M_2 and the empty alveoli for the remaining cheek teeth. *Wakaleo vanderleurei* was distinguished from *W. oldfieldi* (Clemens and Plane, 1974) on the basis of larger molars and dentary size and strong anterior and labial ridges descending from the apical cusp of M_2 . Additional diagnostic characters were given as: P_3 absolutely and relatively larger than in *W. oldfieldi* and the M_2 talonid basin of subrectangular, as opposed to oval, outline. On the basis of the close similarity of the species, Clemens and Plane (1974) considered *W. oldfieldi* to be directly ancestral to *W. vanderleurei*.

Megirian (1986) compared an almost complete *W. vanderleurei* dentary with the *W. oldfieldi* holotype, attributing differences in the dentary shape to evolutionary trends within the lineage. The cranium of *W. vanderleurei* was described by Murray *et al.* (1987).

Existing cranial material of *W. cf. oldfieldi* (Archer *et al.* 1989) has not been described. Subsequently recovered *Wakaleo* material from the Bullock Creek Local Fauna has resulted in a small collection of four well-preserved dentaries, a fragment of maxilla and a few examples of possible wakaleonine postcranial material, including a distal radius showing some features of possible functional significance.

At present, the geochronology of depositionally isolated Tertiary aged vertebrate sites in Australia is determined by the stage of evolution of a small suite of diprotodontoid marsupials (Woodburne *et al.* 1985). Consequently it is important to document the range of variation of significant chronospecies from various localities. The apparent gradual, linear evolution of *Wakaleo* species combined with the increasing evidence that they are not especially rare fossils, may indicate that the wakaleonines are at least as useful for stage-of-evolution geochronology as the zygomatic diprotodontids. The morphological overlap in *Wakaleo* and other chronospecies

(e.g. *Neohelos tirarensis*) from Miocene-aged localities in Australia offers the possibility of a refined geochronological faunal calibration, assuming that the trends are time-related.

Abbreviations used in the text are as follows: CPC, Commonwealth Palaeontological Collection, Canberra; NTM, Northern Territory Museum, Darwin; SAM, South Australian Museum, Adelaide; UCMP, University of California Museum of Paleontology, Berkeley.

SYSTEMATICS

Family Thylacoleonidae

Wakaleo vanderleueri Clemens and Plane

Wakaleo vanderleueri Clemens and Plane, 1974: 656-660, pl. 1, text-fig. 2.

Material. NTM P87108-6, left dentary with P_3 - M_3 ; NTM P87108-5, left dentary with I_1 - M_3 ; NTM P8695-97, right dentary fragment with $M_{3,4}$; NTM P87103-9, left maxilla retain-

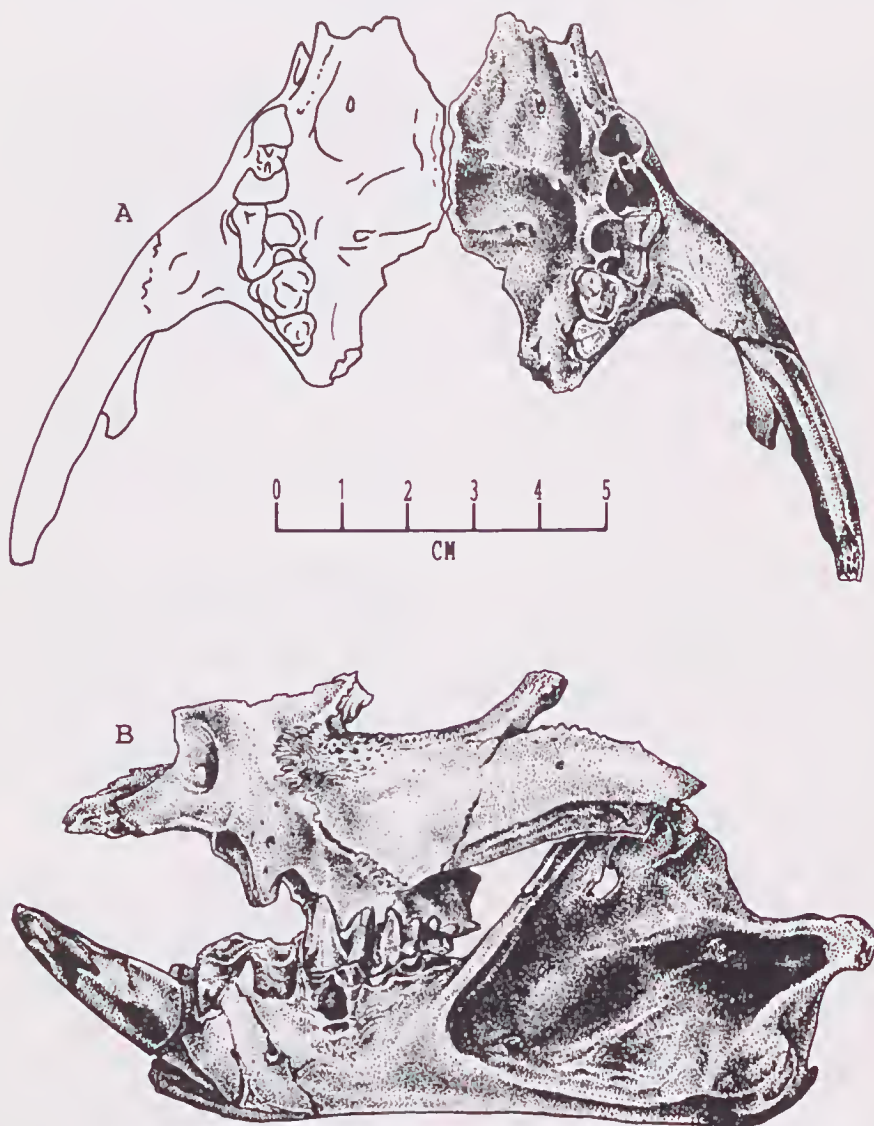


Fig. 1. Newly recovered acetic acid prepared *Wakaleo vanderleueri* cranial material from the mid-Miocene Bullock Creek Local Fauna. A, Ventral aspect of left maxilla (NTM P87103-9) depicted as a mirror-image restoration; B, partial restoration of *W. vanderleueri* skull in lateral aspect combining maxilla (NTM P87103-9) with left dentary (NTM P87108-5). Note heavily worn incisor, eroded alveolar bone below M_2 in dentary NTM P87108-5, complex maxillo-jugal suture and characteristic rugosity of the bone below the orbit in NTM P87103-9.

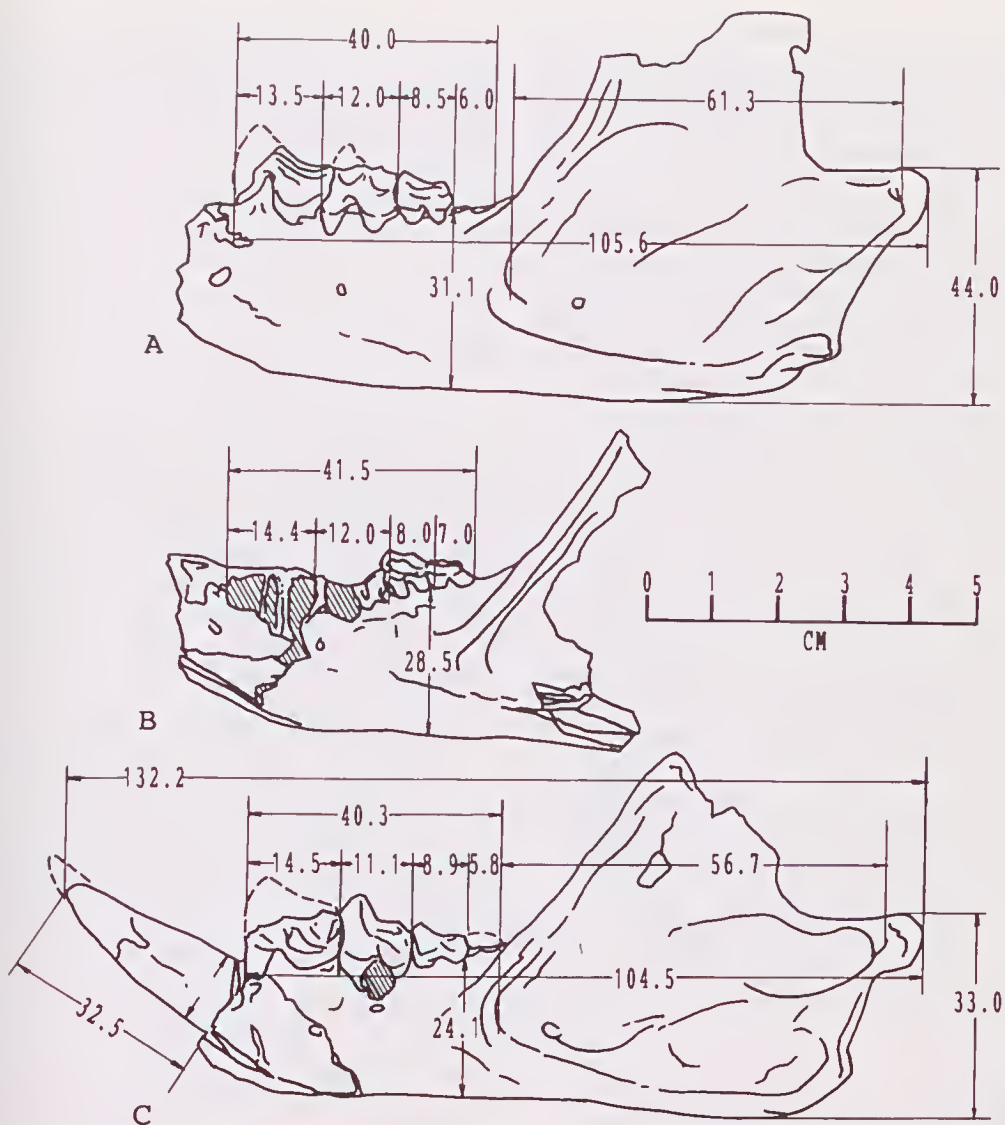


Fig. 2. Variations in size and shape of three *W. vanderleueri* dentaries from the Bullock Creek Local Fauna. A, left dentary NTM P87108-6; B, right dentary NTM P8695-97 (reversed for comparison); C, NTM P87108-5, left dentary resembling the type specimen of *W. oldfieldi* (SAM P17925). Measurements of the teeth give the dimensions of the alveoli, not the tooth crowns, and are not intended to be equated with the crown measurements given in Table 1.

ing M_{2-4} ; NTM P8695-95, distal fragment of left radius; NTM P8695-96, isolated left M_4 .

Age. The Bullock Creek Local Fauna is estimated to be mid-Miocene age (Serravalian Stage); post-Kutjamarpu/ pre-Alcoota (Clemens and Plane 1974).

Description. Maxilla: The maxilla of *W. vanderleueri* has been described by Murray *et al.* (1987). NTM P87103-9 is very similar to CPC 26604. It differs from the previously described specimen in lacking an alveolus for

the P_2 , in having a slightly longer diastema and a smaller canine alveolus (Fig. 1A, B).

Dentaries: The dentary morphology of *Wakaleo* species has already been described in detail by Clemens and Plane (1974) and Megirian (1986). The recently discovered Bullock Creek *Wakaleo* specimens will therefore be considered on a comparative basis by reference to Figures 1B, 2A-C, 3A-C, 4A, B and Tables 1-2. NTM P87108-6 (Fig. 2A) is a robust specimen with a deep horizontal ramus,

shallow masseteric fossa and a weakly developed anteeondylar fossa, a thumb-print sized depression situated within the masseteric fossa, immediately anterior to the condyle. In shape and proportions it strongly resembles the isolated left dentary (NTM P85553-4) described by Megirian (1986), but is distinctive in having a deep anteeondylar fossa and sharply delineated crests surrounding the masseteric fossa. NTM P87108-5 (Fig. 2B) has a much shallower horizontal ramus than either of the above specimens. It is otherwise quite thick, with a marked convexity to its lateral surface. NTM P87108-5 (Figs 1A, 2C, 6C) is remarkable for its gracility, and except for its slightly larger size (about 10%) it is nearly identical to the holotype of *W. oldfieldi* (SAM P17925). It departs from *W. oldfieldi* in having a deep anteeondylar fossa, though other *W. vanderleueri* specimens indicate that this is a variable feature (Fig. 2A; Table 2).

Lower incisor: NTM P87108 (Fig. 3A-C) retains the I_1 , which was previously unknown for the species *W. vanderleueri*. Although very worn at the tip, the incisor is much like that of *W. oldfieldi*. The enamel crown envelopes the entire apical portion of the tooth. The incisor has a flattened, asymmetrically elongated, oval section. The distinctly triangular shape of the lower incisor crown of *Thylacoleo carnifex* is scarcely, if at all, apparent in *W. van-*

derleueri. The ventral contour of the tooth is a smooth arc, that if projected beyond the worn tip of the crown, would result in the slightly hooked caniniform shape, distinctive in *W. oldfieldi*. This assumption is also supported by the orientation of the breached nerve canal. The dorsolabial enamel flange that was apparently present is entirely worn away in the specimen. The lingual surface of the tooth is flat and presents a well-developed interproximal wear facet over the distal third of the tooth. This indicates considerable mobility of the dentaries at the symphysis.

The extensive wear on the crown of the incisor of NTM P87108-5 indicates that *Wakaleo* dentitions were involved in more than puncturing wounds, breaching the hides of their prey and slicing off chunks of flesh. The crown is deeply worn dorsally exposing a considerable length of the cementum, dentine and nerve canal. The wear continues around the apex of the crown extending along its ventral surface for at least 5.0 mm.

Lower cheek teeth: The condition of the lower cheek teeth of *W. vanderleueri* also seems to indicate extremely hard usage, which is not restricted to observations of considerable P_3 crown attrition. Two of the four examples have apical abscesses around the P_3 roots. NTM P8695-97 appears to have had a condition similar to "lumpy-jaw". These

Table 1. Dimensions of the cheek dentitions of *Wakaleo* spp (in millimetres). Data is taken from Clemens and Plane (1974), Megirian (1986), Murray *et al.* (1987), and Archer and Rich (1982). Brackets indicate estimated dimensions.

SPECIES/NUMBER	CHEEK DENTITION - LOWER											
	P_3			M_2			M_3			M_4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
<i>W. oldfieldi</i>												
SAM P17925	12.4	6.2	7.8	10.4	8.7	7.2						
UCMP 102677							7.5	6.3	6.1			
<i>W. vanderleueri</i>												
NTM P87108-6	[14.2]	6.3	7.6	11.3	[8.5]	7.7	9.4	6.3	6.8			
NTM P8695-97							8.2	6.6	6.2	6.0	4.2	4.7
NTM P87108-5	[14.5]	5.7	7.2	12.0	8.2	7.4	9.8	6.3	6.1			
NTM P8695-96										5.8	4.1	4.0
CPC 13527				11.7	7.9	7.7						
NTM P85553-4	13.9	—	[7.1]	9.6	—	[6.5]	7.6	5.5	5.2			
	CHEEK DENTITION - UPPER											
	P_3		M_2		M_3		M_4					
	L	W	L	W	L	W	L	W				
<i>W. vanderleueri</i>												
CPC 26604	17.9	9.2	11.2	11.0	7.0	9.5	5.0	5.5				
NTM P87103-9					7.5	8.4	5.6	5.8				
<i>W. alcootaensis</i>												
NTM P1	24.4	9.9	14.7	15.7	7.2	9.0						

Table 2. Summary of character expressions in *Wakaleo* spp. Symbols used: +, present; -, absent; ?, unknown.

CHARACTER	SPECIES		
	<i>W. oldfieldi</i>	<i>W. vanderleueri</i>	<i>W. alcootaensis</i>
Small p_3	+	-	?
Cheek teeth wide	+	-	?
Crest on m_2	-	+?	?
Oval talonid basin	+	+-	?
Antecondylar fossa	-	+-	?
Masseteric crests	+	+-	?
Subcondylar fossa	-	+	?
Gonial angle	-	+-	?
Dentary depth	-	+-	?
Pterygoid fossa	-	+-	?
Posterior strut	-	+	?
P_2	+	+-	-

pathological signs were probably caused by impactions of bone splinters and extreme occlusal forces being exerted on the roots.

The dimensions of *W. vanderleueri* cheek teeth vary, (Table 1) and in some instances closely approximate or overlap with those of *W. oldfieldi*. Although no complete *W. vanderleueri* P_3 is available, the NTM P85553-4 example is at least 1.5 mm longer than that of the *W. oldfieldi* type. The estimated lengths of the other two *W. vanderleueri* P_3 's support the observation that a longer P_3 is consistent for the species. The differences between the *W. oldfieldi* holotype and our sample of *W. vanderleueri* can be accentuated somewhat by comparing proportional differences between cheek tooth lengths and widths (McGirian 1986) but even here, the distinction is relatively minor (Fig. 4A, B). Such a difference could be attributed to individual variation, to allometry or could relate to sexual dimorphism. The overall differences between the two species in evidence so far could be duplicated in contemporaneous geographic morphs in many widespread mammalian species, eg. among geographic races of *Trichosurus vulpecula*.

Other possible distinctions between *W. oldfieldi* and *W. vanderleueri*, the subrectangular talonid basin and strong anterior and labial ridges on the apical cusp of M_2 are not supported by the additional material. Due to wear, the existence of a consistent labial ridge on the M_2 of any specimens other than on that of CPC 13527 (Clemens and Plane 1974) has not been verified. The subrectangular talonid basin observed in CPC 13527 is a variable feature: both NTM P87108-6 and NTM P87108-5 have oval talonid basins, as in *W. oldfieldi*.

Distal radius fragment: The postcranial skeleton of *Wakaleo* species is largely un-

known. Foot elements of thylacoleonids have been recovered from the Alcoota Local Fauna that probably represent *Wakaleo alcootaensis*. The only material of a distinctive nature that can be confidently assigned to *Wakaleo vanderleueri* is a radius fragment (NTM P8695-95). We describe this specimen because it appears to express some functional contrasts with both *Priscileo* and *Thylacoleo*.

The specimen consists of approximately one-third of the distal end of a left radius within the size range expected for an animal with a skull the size of *Wakaleo* (Fig. 5A-C). Its distinctive thylacoleonid features include a broad, flattened distal diaphysis, anteroposteriorly compressed, shallow scapholunar articular surface, prominent, pointed styloid process and prominent ulnar process (DeVis 1900).

The crests and surfaces for muscle and connective tissue attachments on the fragment are interpreted in relation to Barbour (1963) for the brushtailed possum (*Trichosurus vulpecula*) and Rauscher's (1987) interpretation of *Priscileo*. The anterior surface of the

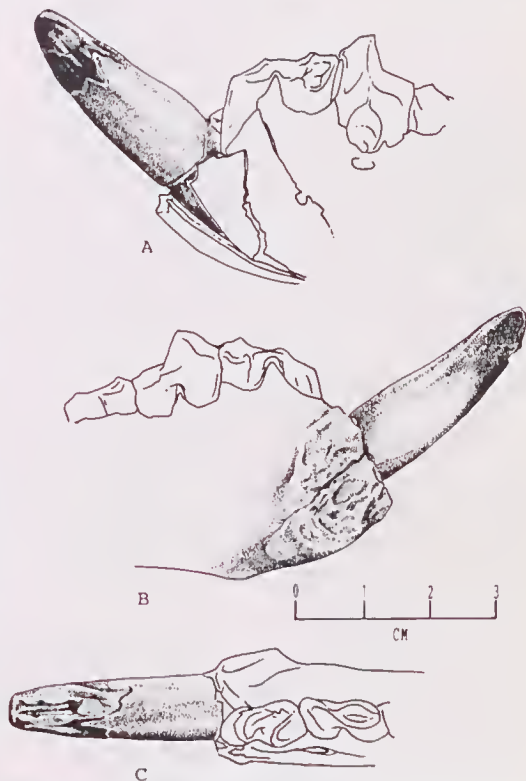


Fig. 3. Left I_1 of *Wakaleo vanderleueri*. A, labial aspect; B, lingual (interproximal) aspect; C, dorsal aspect.

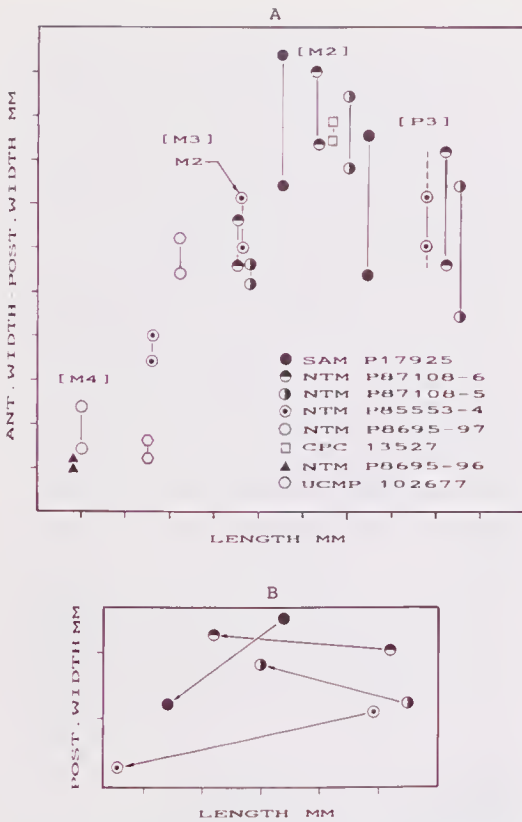


Fig. 4. Scatter diagrams of lower cheek tooth dimensions in *Wakaleo* spp. A, Linear plot of tooth-length by anterior width and posterior width, the latter two dimensions being depicted by connecting them with a vertical line - species designations of specimens listed by accession numbers are given in Table 2; B, log-linear plot of P_3 and M_2 - arrow draws attention to the trending relationship of length to width ratio of P_3 to M_2 for each specimen. Symbols correspond to the key for graph A. Because many of the teeth are imperfect, the graph depends upon estimates. These are designated in Table 1 by brackets.

fragment is slightly convex. On the ulnar side of a low crest, a broad, shallow concavity is present for the extensor carpi radialis and extensor digitorum communis tendons. The fragment preserves a groove for the attachment of the abductor pollicis longus and extensor pollicis brevis tendon anterodorsal to the styloid process.

The styloid process is triangular with its apex directed posteriorly. The posterior surface of the styloid process bears a triangular facet which participates in the formation of a shallow, shelf-like crest dorsally for the attachment of the radiocarpal ligaments. The crest for the radiocarpal ligaments ("posterior crest" of Rauscher 1987) is robust and extends across the epiphysis in a shallow arc.

Immediately dorsal to the styloid process, a tuberosity, apparently for restraining the abductor pollicis tendon is conspicuously developed (Fig. 5C, *apl. br?*). Its degree of development suggests that the brachioradialis probably inserted on the dorsal surface of the tuberosity rather than on the dorsal aspect of the scaphoid. The ulnar articular surface is

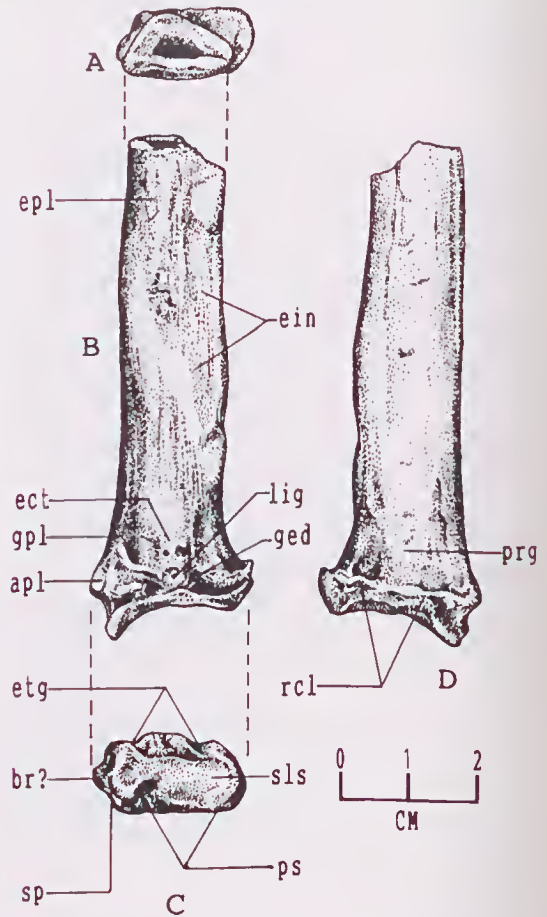


Fig. 5. Distal left radius fragment (NTM P8695-95) considered by the authors to represent *Wakaleo vanderleueri*. A, section viewed from the proximal end of the fragment; B, extensor side; C, distal aspect showing scapholunar articular surface; D, flexor side. Abbreviations relating to inferred muscles and ligamentous scars: *epl*, extensor pollicis longus; *ect*, extensor carpi tendons; *apl*, abductor pollicis longus and extensor pollicis brevis (extensor ossi carpi pollicis); *etg*, grooves for extensor tendons; *br?*, probable insertion of the brachioradialis muscle (as in anthropoid primates?); *sp*, styloid process; *sls*, scapholunar surface; *ged*, groove for extensor digitorum communis tendon; *lig*, ligamentous scar; *ein*, scar of extensor indicis or extensor pollicis (brevis?); *prg*, groove for the pronator muscle; *rcl*, crest for the radiocarpal ligaments; *ps*, posterior shelf; *gpl*, groove for extensor pollicis longus.

smooth and convex and not directed obliquely posteriorly. A flattened area of the anterior diaphysis about 25.0mm from the articular

surface appears to represent the distal origin of the extensor pollicis. A low crest divides this surface, implying the incipient differentiation

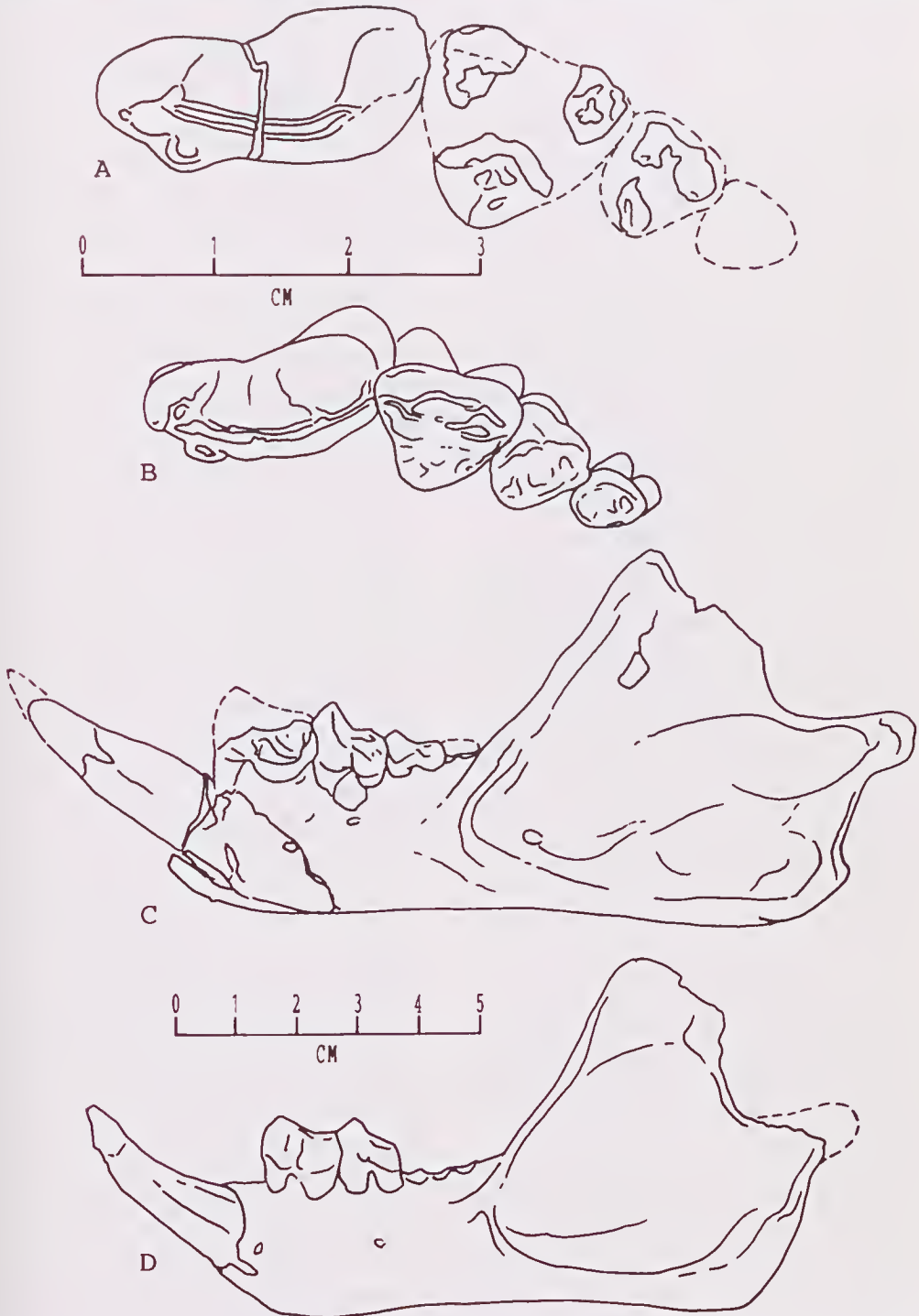


Fig. 6. Sealed outline sketches of the three *Wakaleo* species. A, upper cheek teeth of *W. alcootaensis*, (after Areher and Rieh 1982); B, upper cheek teeth of *W. vanderleueri*, CPC 26604, (after Murray *et al.* 1987); C, dentary of *W. vanderleueri*, NTM P87108-5; D, dentary of *W. oldfieldi*, SAM P17925.

of the pollical extensors as observed by Rauscher (1987) for *Priscileo*. The thin, flange-like expansion on the mesial border of the fragment represents the area of attachment of the interosseous membrane.

Comparing the three known thylacoleonid genera; the distal articular surfaces show increasing anteroposterior compression in the order: *Priscileo*, *Wakaleo*, *Thylacoleo*. This is largely due to the reduction of the posterior crest of Rauscher (1987) and appears to be related to the range of movements of the wrist joint, determined in part, by the radiocarpal ligaments.

The broader, arcing radiocarpal ligamentous attachment in *Priscileo* appears to have provided strong resistance to tensional forces on the wrist joint over a wide range of radiocarpal postures, indicating considerable wrist mobility. Tensional resistance combined with mobility is also reflected in the more elongated and robust styloid process for the attachment of the radiocollateral ligaments.

The radiocarpal articulation is more hinge-like in *Thylacoleo* than in the other two genera, the *Wakaleo* specimen being intermediate. We conclude that *Wakaleo* was less agile than *Priscileo*, but this does not exclude the possibility that *Wakaleo* was arboreal: its wrist joint places it well within the range of a scansorial climber, but might reasonably exclude it from the terminal branch gymnastics that *Priscileo* would have been capable of.

Remarks. Megirian (1986) supported Clemens and Plane's (1974) species diagnosis of *W. vanderleueri* by confirming the presence of a relative and absolute enlargement of the P_3 compared to M_2 in the second, more complete Bullock Creek specimen (NTM P85553-4) from the Northern Territory Camfield Beds. The Camfield specimen failed to confirm Clemens and Plane's (1974) observation of the presence of a subrectangular as opposed to oval talonid basin and the presence of strong anterior and labial ridges descending from the apical cusp of M_2 .

The specimen, moreover, exhibited a suite of characters that seemed to enhance the proposed specific designation. These additional, potentially diagnostic characters include the elaboration of the masseteric fossa by a deep oval depression anterior to the condyle and a conspicuous oval depression immediately below the condyle. Megirian (1986) related

these details to a proportionally enlarged adductor complex and a capacity for increased gape. The combination of these and other features resulted in a strongly contrasting visual impression of the two specimens and there seemed to be little doubt that the two species could be consistently distinguished by comparative inspection.

The new Bullock Creek dentary specimens of *Wakaleo vanderleueri* indicate that the distinctions from *W. oldfieldi* are more subtle and probably less reliable than originally thought. Specimen NTM P87108-5 exhibits the slender horizontal ramus, steeper gonial angle and overall proportioning of the *W. oldfieldi* holotype as faithfully as might be expected of any conspecific (Figs 1B, 3C, 6D). It differs only in being slightly larger, on the order of about 10% overall, although like NTM P85553-4 (Megirian 1986; Fig. 1) it possesses a deep antecondylar fossa. However, a larger, more robust *W. vanderleueri* specimen (NTM P87108-6), similar to NTM P85553-4 has a poorly developed antecondylar fossa, no more conspicuous than that of SAM P17925, the *W. oldfieldi* holotype.

Other characters found to merge between the two species include the expression of an oval talonid basin in the M_2 of *W. vanderleueri* and the variable relative proportions of the cheek dentitions (Table 1). Although our Bullock Creek sample is too small for probability testing, the considerable morphological variability of the population is readily apparent. The combined *Wakaleo* spp. show a similar range of variation to some other taxa from these Miocene localities, particularly the widespread zygomaturine diprotodontid *Neohelos tirarensis*. The larger *Neohelos* from the Bullock Creek Local Fauna was initially thought to be specifically distinct from the Tirari, Wipajiri and Riversleigh populations. Re-examination of these populations demonstrates that the variations within a local fauna are about as great as the differences between local faunas. In the absence of any discrete morphological criteria upon which to base a specific differentiation, we conclude that *W. vanderleueri* represents a slightly larger and perhaps younger extreme of the chronocline of *W. oldfieldi* populations.

Wakaleo alcootaensis (Archer and Rich 1982) is also a very similar species (Fig. 6a). Unfortunately, no lower dentitions have been

recovered. The maxillary fragment is morphologically similar to *Wakaleo vanderleuri* but is about 25% larger. The ratio of P_3 to M_2 length is the same as in *W. vanderleuri* and the width to length proportions of the P_3 are almost identical. Judging from what is available for comparison, *Wakaleo alcootaensis* retains all the essential features of the smaller *Wakaleo* species while revealing no characters that would suggest an ancestral relationship to any other thylacoleonid taxa, nor any significant morphological difference, other than larger size that would indicate any deviation from the adaptive zone of its ancestral population. Archer and Rich (1982) observed that $P_{1,2}$ are absent in the Alcoota specimen. *Wakaleo vanderleuri* shows that the presence or absence of the P_2 is variable by virtue of its absence in a newly acquired specimen (NTM P87103-9) and the presence of the tooth in CPC 266904 (Murray *et al.* 1987); (Table 2). Thus the grounds for discriminating *W. alcootaensis* from *W. vanderleuri* rest predominately, if not entirely upon its larger size and the inference of its younger geological age.

The absence of a clear morphological distinction other than size among these species is by no means an unusual situation in the Australian marsupial fossil record, where the phenomenon of "morphic" speciation is a familiar theme in later Tertiary assemblages. In Quaternary faunas, a consistent size difference of about 25% or more between two otherwise morphologically identical populations has, more often than not, resulted in the designation of separate species (for example see Bartholomai 1975 for a discussion of the differences among *Macropus giganteus*, *M. titan* and *M. birdselli*).

On the basis of the available evidence we consider that the priority designation *Wakaleo oldfieldi* (Clemens and Planc, 1974) is the systematically valid species, whereas *W. vanderleuri* represents a chronospecies, the discrimination of which will ultimately depend upon arbitrations of the morphocline extending to *W. alcootaensis*.

In the case of *W. alcootaensis*, a poorly preserved specimen, there is some reservation in equating the degree of molar reduction relative to the premolar with that of *W. oldfieldi* and there is substantial evidence in support of its significantly younger geological age (probably two to three million years younger

than Bullock Creek), whereas an age difference between the Wipajiri Formation and the Camfield Beds is difficult to demonstrate other than by the minor differences implied by comparable elements of their respective faunas.

We recognize the utility of formally designating chronospecies in palaeontology and support the need for making such discriminations, but draw attention to the problematic genetic and phylogenetic implications, and more importantly, the assumption that geographic distance and crudely interpolated geological age differences provide a sufficient basis for a species separation. In this particular case, the subtle differences between the Bullock Creek and Wipajiri specimens give the impression of a gradually evolving form and thus, the basic idea put forth by Clemens and Planc (1974) will probably be supported by new evidence. The problems arise when *Wakaleo* material, particularly in the form of isolated fragments, is eventually recovered in a new locality and the geochronology of the site becomes founded on the basis of little more than the size of a tooth.

Wakaleo cf. oldfieldi is also known from the Carl creek Limestone at Riversleigh, Queensland. Archer *et al.* (1989) consider their specimens to be intermediate between the Wipajiri and Etadunna equivalents. A possible earlier *Wakaleo* sp. specimen has been recently recovered from Riversleigh (Mike Archer, personal communication). It is among the earlier forms of *Wakaleo* that we might anticipate some significant morphological distinctions, perhaps with connections to *Priscileo* or *Thylacoleo*.

DISCUSSION

Wakaleo phylogeny. Although *Wakaleo*'s cheek dentition is more derived than that of *Priscileo* Rauscher 1987, the retention of an alisphenoid tympanic wing in *Wakaleo* indicates that its basicranium is the least derived of the known thylacoleonids and moreover, leaves the question open as to a possible phalangeridan affinity for the group (Murray *et al.* 1987). Thylacoleonids are clearly an ancient group, with no especially close affinities to any of the living Australian marsupials. Since the time of Owen, the overall similarity of the thylacoleonids to various phalangeridan

groups (burramyids, petaurids and phalangerids in particular) has been recorded.

It is therefore with some trepidation that Aplin and Archer (1987) placed the thylacoleonids within the Vombatimorphia, explaining that the essential phalangerid characters of thylacoleonids are either plesiomorphic or parallel conditions. In fact, there are few unequivocal vombatimorphian synapomorphies in evidence in *Wakaleo*, whereas *Thylacoleo carnifex* supports their observations remarkably well (Murray *et al.* 1987).

Speculating on what is known so far of the group, it can be assumed that the ancestral thylacoleonids were about the size of brush-tailed possums and basically similar in appearance. They were arboreal, based on the morphology of the limb fragments of the small mid-Miocene *Priscileo pitikantensis* (Rauscher, 1987) and the proportions of complete skeletons of the derived Pleistocene form *Thylacoleo carnifex* (Wells and Nichol, 1977; Finch 1982). Our current knowledge of the family commences in the lower to mid Miocene, when both *Priscileo* and *Wakaleo* were present in the tropical forests of northern Australia.

Speculations on predaceous macropodoids aside, the medium to large bodied marsupial carnivore guild in Australia had not elaborated to the extent seen among placental mammals of equivalent age. In the mid-Miocene, the thylacoleonids are represented by the two genera, *Wakaleo* and *Priscileo*; The genus *Thylacoleo* is not yet in evidence. Our examination of the wrist joint of *Wakaleo* suggests a possible partitioning of the two genera, with *Priscileo* being an arboreal form. The heavily worn dentitions and root trauma in *Wakaleo*, suggestive of scavenging, might be taken as evidence of a terrestrial adaptation.

Other mid Miocene terrestrial carnivores include a minor radiation of small thylacinids, among them, the genus *Nimbacinus* Archer *et al.*, 1989. There appears to have been therefore, a simple carnivore guild spanning the arboreal and terrestrial adaptive zones in the predominately forested environments postulated for the mid Miocene of Australia. As these once coterminous forests became increasingly dissected by invading savanna grasslands in the later part of the Miocene, the partitioning of the carnivorous marsupial genera was accentuated. A fox-like forest

thylacinid gave rise to the larger, cursorial, savanna adapted genus *Thylacinus* which makes its appearance in the late Miocene Alcoota Local Fauna. The genus *Wakaleo* retained its progressively diminishing forest-edge adaptation, while *Priscileo* retreated with the forests to eventually become extinct, though not before giving rise (vicariantly) to a scansorial, semiterrestrial descendant, similar to *Wakaleo*. This mid- to late-Miocene thylacoleonid was the ancestor of *Thylacoleo carnifex*.

The first representatives of *Thylacoleo* (*Thylacoleo*) *hilli* Pledge, 1977 were about the same size as *Wakaleo alcootaensis* and may have been contemporaneous. As *Thylacoleo* species developed a stronghold in the forested east of Australia, *Wakaleo* may have become trapped in a diminished and deteriorating habitat by early Pliocene times and being unable to take refuge elsewhere due to competition from *Thylacoleo*, became extinct.

Assuming that our geochronological assessments of the relative ages of the Miocene Local Faunas are correct, *Wakaleo* appears to retain the same adaptive zone throughout its existence. It appears to be a slowly evolving form in which its primary modification is enlargement. A similar pattern is evident in certain other Miocene genera such as *Neohelos* and *Palorchestes*.

SUMMARY AND CONCLUSIONS

The Miocene genus *Wakaleo* contains three species of which one, *W. vanderleueri* shows few unequivocal distinctions from the nominal species *W. oldfieldi*. Because of the uncertainty of the geological ages of local faunas from which these forms were recovered, the assumption that the slightly larger *W. vanderleueri* represents a different species on chronological and geographic grounds alone is unsupportable. The increased sample size of *W. vanderleueri* from the Bullock Creek Local Fauna points to a full morphological overlap with the Wipajiri specimen, analogous to the continuity observed in certain other species such as *Neohelos tirarensis*.

Wakaleo alcootaensis is too fragmentary to place under the same scrutiny. Its only distinction other than larger size from the Bullock Creek *Wakaleo* was the absence of P_2 . Agensis of the P_2 is also found in the Bullock Creek

sample. There is abundant evidence however, to indicate that the Alcoota Local Fauna is significantly younger than either the Camfield Beds or the Wipajiri Formation. Moreover, the Alcoota species is about 25% larger than the largest Bullock Creek *Wakaleo*, a degree of difference often used to distinguish species of Pleistocene "giant" marsupials from their living counterparts (eg. *Macropus titan* from *Macropus giganteus*; *Sarcophilus harrisi* from *Sarcophilus lanianus*). The character of the Alcoota Local Fauna differs from all of the other Miocene local faunas in showing a marked increase in body size among many of its species, particularly in the case of the thylacines and the zygomaturine diprotodontids. Descendants of mid Miocene lineages from Alcoota also show morphological distinctions more appropriately designated as being generic.

The *Wakaleo* sample now at hand suggests a population continuity over a geologically significant period of time. Within the genus, there is a general conservatism of morphological features, with possibly only average size varying significantly through time. A fossil population showing monotonic variation of a single character or a restricted suite of characters is more realistically described as a single chronospecies rather than a number of species distinguished by provenance and arbitrary subdivisions of a morphocline. Nevertheless, the designation of chronospecies has utility in biochronology. Clemens and Plane (1974) recognized the probable population continuity of *W. vanderleueri*, which we recognize, together with *W. alcootaensis* as chronospecies, but only *W. oldfieldi* has phylogenetic validity.

Observations on the radius fragment assigned to *Wakaleo* indicate that its radiocarpal ligaments restricted the wrist mobility of *Wakaleo* more than in *Priscileo*. *Thylacoleo* shows a greater restriction of wrist movement than either of the other genera. The wear on the incisor and evidence of damage to the gums and alveoli of *Wakaleo* suggest that it was as much a scavenger as a predator. This pattern may indicate an at least partially terrestrial adaptation.

Speculation on the evolution of *Wakaleo* raised the possibility of wakaleonines being the more plesiomorphic members of the family and that *Thylacoleo* may have arisen vicari-

antly from *Priscileo* as it retreated eastwards with the diminishing forest cover of later mid Miocene central Australia.

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